Notes on the Life Cycle and Natural History of Butterflies of El Salvador. I C.-*Colobura dirce* L. (Nymphalidae-Coloburinae)

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Abstract: All stages and instars of *Colobura dirce* L., as studied in the vicinity of San Salvador, El Salvador, Central America, are described and illustrated photographically. The larval foodplant was *Cecropia mexicana* Hmsl. Larval and adult behavior are also described. Comparisons are made of various stages of *C. dirce* and those of some more or less similar Nymphalidae, especially of the genera *Smyrna*, *Historis* and *Coea*, which belong in the Coloburinae, and not in the Limenitinae. The name "adenosma" is proposed for the ventral, eversible, odoriferous prothoracic gland present in *C. dirce* larvae, and comparable, if not homologous, to the similar structure found in many families of Lepidoptera.

This is the beginning of the fourth series of articles presenting our observations on the life cycle, larval foodplants and behavior of the early stages and adults of butterflies found in El Salvador. The present series will deal with the species of the Nymphalidae which have been grouped by different authors under the subfamily Gynaeciinae or, more rightly, Coloburinae. We think it is only fair to begin the series with the species from which that name was taken: *Colobura dirce* L.

On September 14th, 1969 we found for the first time, on a leaf of "Guarumo," a group of three larvae, velvety black, with a row of yellow spots along the spiracular area, white and yellow branched spines on the body and long horns on the black head, which pupated two days afterwards. On September 29 the adults emerged and we then realized that they were *Colobura dirce*. Since then we have reared the species a number of times starting from recently deposited eggs. The rearing has been effected in transparent plastic bags, tightly sealed with rubber bands, from which excess moisture and excreta were cleaned daily. The foodplant was replaced at the most every second day, as otherwise the larvae die when fed on even slightly decaying leaves. When pupation occurred the specimens were transferred to a wooden cage, with mosquito-net windows, where the adults emerged. Even though we are aware that under natural conditions there might be appreciable difference we kept records of the time elapsed in the different stages of the metamorphosis and

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of the sizes of them. Photos have been taken of the whole process and specimens preserved in alcohol, which have been sent to the American Museum of Natural History, New York. Bags and pupation box were kept indoors under ambient light and temperature conditions.

LIFE CYCLE STAGES

Egg (Fig. 1). Spherical, 1 mm diameter, dark olive-green with 11 prominent whitish-green ribs running vertically from the base, fading at the micropylar zone leaving an empty circular space where the micropyle is clearly visible. They hatch in 4 days.

First instar larva (Fig. 2). Head dark brown, slightly cordiform, with sparse thin setae. Body cylindrical, light brown when recently hatched, with sparse thin and short setae implanted on tiny conical black chalaza. Turns dark greenish-brown after feeding from the leaf and then discolored warts are clearly visible on thoracic segments 2 and 3, and abdominal segments 2, 4, 6, 8 and 9. Two mm long when hatching, about 4 mm when ready to moult in 3 days.

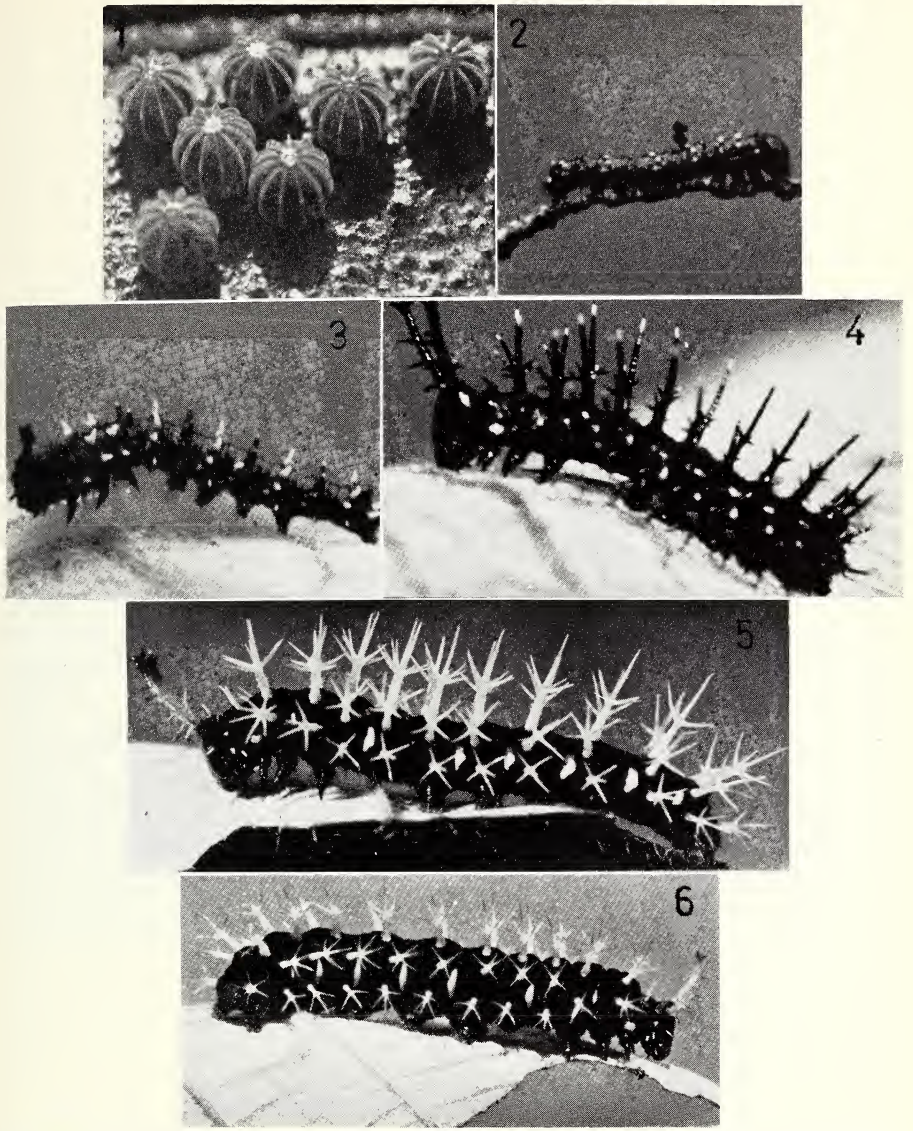
Second instar larva (Fig. 3). Head black with short, stubby horns, one on each epicranium, and armed with tiny secondary spines bearing thin setae. On the lateral borders of the head, several tiny spinulets each with a thin seta at the tip. Body cylindrical, dark brown or black, with short conical spines on all segments but 1st thoracic, which has a cervical shield with 8 spinulets. Second and third thoracic segments with subdorsal and supraspiracular, conical spines. Each abdominal segment has an additional subspiracular spine except 8th and 9th, which have the subdorsal spines only. Each of these spines bears a seta distally. The thoracic spines and the abdominals on 2nd, 4th, 6th, 8th and 9th segments are white, the rest dark brown, as are the legs and prolegs. Grows to about 7.5 mm in 3 days.

Third instar larva (Fig. 4). Head shiny black with long diverging horns (longer than head) armed with accessory spines placed in the following order: one near the base directed anterad, closely followed by three placed at the same level, two directed inwards (at an angle), one outwards; slightly higher another one parallel to the basal one, and finally a sixth directed inwards. Each horn ends distally in a knob crowned by five spinulets. Each lateral margin of the head shows two whitish small spines, fronted by a single black one. Between the horns and close to their bases, there is another small spine. The body is now shiny black also, with a row of white spots along spiracular area, starting on first thoracic segment, ending on 8th abdominal segment. On the cervical shield one of the lateral spinulets has grown about three times as big as the rest. All the spines on the rest of the body are quite long, black with light tips, and about the middle of the shaft each is armed with a rosette of secondary spines. The rosettes on the thoracic segments have 5 points, the rest have 4. Grows to 12 mm in 2 days.

Fourth instar larva (Fig. 5). Head as in third instar with longer horns, which are yellowish with black tips, and the lateral spines white. The body velvety black and spines bright yellow, the same as the spiracular row of spots. Grows to 25 mm in 6 days.

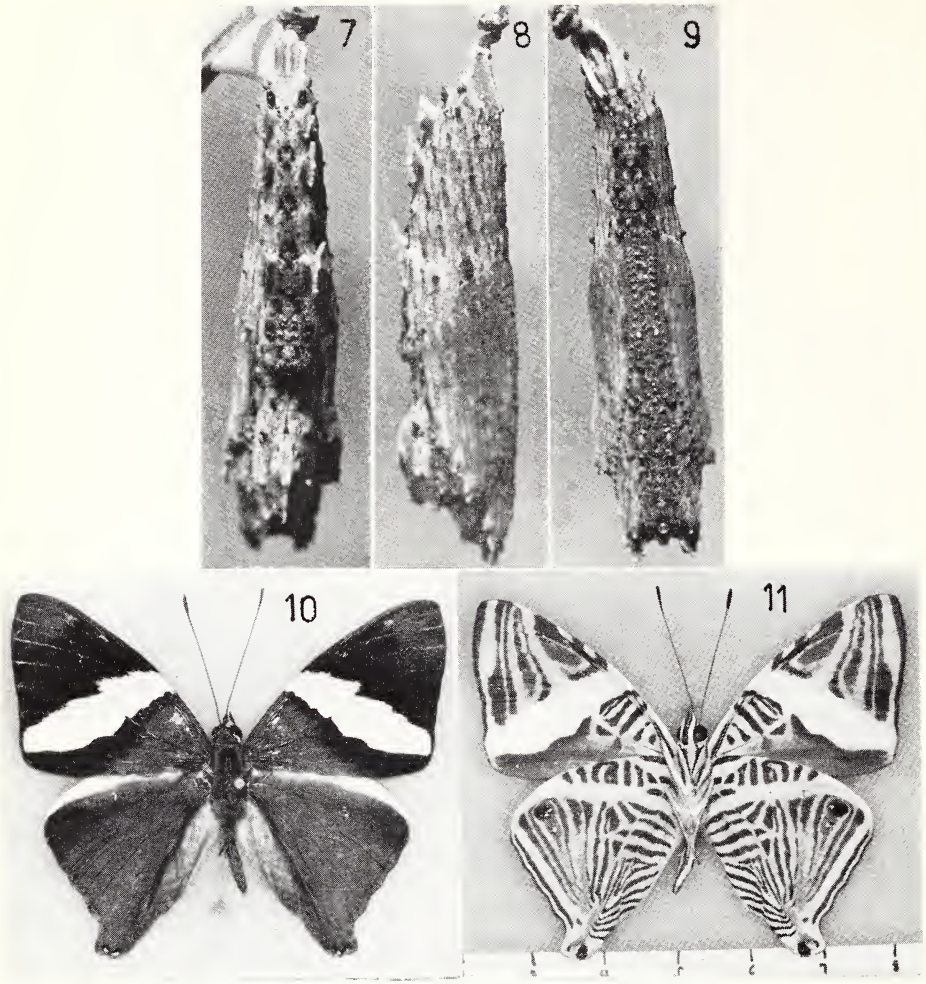
Fifth instar larva (Fig. 6). Head black with white, brown-tipped horns. Just after moulting, all spines on the velvety black body are yellow, but by the following day all thoracic spines become white, while the abdominals stay bright yellow. The spiracular row of spots also remains bright yellow. Body much thicker than head. Grows to 35–38 mm in 7–9 days.

Prepupa. No color changes. Hangs with thorax incurved ventrally for 1 day.



Figs. 1 to 6. *Colobura dirce* L. 1. Eggs. Actual diameter about 1 mm. 2. First instar larva on resting perch. Notice frass pellets on the body. Actual length about 3 mm. 3. Second instar larva. Length about 7 mm. 4. Third instar larva. Length about 10 mm. 5. Fourth instar larva. Length 25 mm. 6. Fifth instar larva. Length 36 mm.

Pupa (Figs. 7–9). Cylindrical, long and thin. Light brown colored with more or less dark brown markings dorsally along meson and between wingcases. Looks in all respects like a dried piece of broken twig. On the head two ragged short prolongations following the axis of the body. Thorax slightly keeled bearing paired warts at the sides. A faint depression



FIGS. 7 to 11. *Colobura dirce* L. 7. Pupa dorsal view. 30 mm long. 8. Pupa lateral view. 30 mm long. 9. Pupa ventral view, showing movable segments. 30 mm long. 10. Adult, dorsal aspect. 11. Adult, ventral aspect. Scale in cm.

separates thorax from abdomen, which has on 4th, 6th and 7th segments short paired spines, directed posterad, mounted on winged bases. Smaller winged appendages are on 8th and 9th segments. The cremaster is very wide laterally, ending in a pointed, crochetted knob. The abdominal segments that are not provided with appendages show subdorsally small warts, same as supra- and subspiracularly, from the wing cases to 9th abdominal segment. Spiracula inconspicuous brown. Ventrally there are paired warts from 6th to 9th abdominal segments. The beaded antennae and proboscis covers form a rough-looking area from head to 6th abdominal segment, limited laterally by the smoother wingcases. Measures 28 to 30 mm long, 6 mm wide at widest points. Duration 12–14 days.

Adults (Figs. 11–12). Both males and females with same color pattern and same wing-shape. Forewing with a slightly convex costal margin to faintly pointed apex, shallowly S-shaped outer margin to rounded tornus, straight inner margin. Hindwing with convex costal margin, rounded outer angle, obliquely inwards, straight and faintly sinuose outer margin, short and thick tail-like projection at anal angle, straight inner margin with a fold. Colors dorsally: forewing dark grayish-brown basally, black apically, separated by a wide slanting light yellow band, which covers from tornus to mid-costal margin. This light yellow band turns darker as the individuals get older. Hindwing uniform dark grayish-brown with discolored narrow edge along costal margin and discolored inner fold. Two small bluish spots on tip of stubby tail. Ventrally forewing shows a discolored replica of the dorsal yellow band, surrounded by dark brown stripes, on cream ground color, some parallel to the band (basally), some almost perpendicular to it (distally). Hindwing pattern a complicated array of brown stripes on cream ground color with a thin band almost parallel to costal margin, two small eye-like spots of black, rusty red and blue close to outer angle, and two small spots on the tip of the short tail. Body, dorsally and ventrally, concolored to the respective wing surface. Eyes and proboscis brown, antennae white and brown ringed, orange tipped. Wing span about 60 mm, females being slightly larger than males.

Total developmental time under laboratory conditions, 31 to 35 days. Many individuals succumb to food poisoning, apparently, when the foodplant is slightly decaying. In the field tachinid flies are often a cause of mortality.

NATURAL HISTORY

The adults of *Colobura dirce* are very swift flyers producing a rustling noise audible from a short distance. They frequent wooded ravines, close to wooded coffee plantations, usually flying at tree-top level. They alight on tree-trunks, wings folded, head usually pointing down, and dash readily to other butterflies flying in their neighborhood, even though they are not as pugnacious as their apparently closely related species *Historis odius* and *Smyrna* spp. They even seem to get along with *Catagramma pitheas* Latreille which shares their habitat. We have observed very often, on a particular hill close to Los Chorros (about 10 km from San Salvador), that males will show up at the top of the hill from 12:30 to 13:00 hrs. and will dash from tree to tree, occasionally chasing other butterflies until about 16:30, when they move to lower areas. We have never seen adults visiting flowers. They are often seen feeding on sap oozing from tree wounds, at times on fecal matter, decaying fruits and mud puddles.

The females deposit their eggs in irregular groups, ranging from 1 to 10, on the upper or on the undersurface of "Guarumo" leaves. There seems to be no preference as to the age of the leaf, as we have found eggs on very young and on mature leaves. They do seem to prefer young trees: many times we found eggs and larvae on trees less than 1 m tall, and even on seedlings, with leaves not yet fully formed, less than 30 cm high.

The larvae upon hatching eat the upper part of the eggshell and leave the walls untouched. If they come from a group of eggs the young larvae move together to the nearest edge of the leaf. Remaining close to each other they

start feeding on it and each one constructs a resting perch with frass pellets. They maintain the perch-making habit throughout the following two instars. During 4th and 5th instars they usually stay on the underside of the leaves. While they still make the perches, they start making them at longer distances from each other as they grow but still on the same leaf. The group might dissolve altogether during the late instars. The larvae, even first instar ones, gnaw the prominent ribs at short intervals on the undersurface, apparently to control the flow of plant fluids on the tissues they are consuming, somewhat similar to what we have witnessed in *Danaus* spp. feeding on *Asclepias*, in *Lycorea ceres* when feeding on *Carica papaya*, various Heliconiidae feeding on Passifloraceae, and even some Sphingidae feeding on *Euphorbia pulcherrima* Willd. When several large larvae are congregated on the same leaf, this gnawing of the ribs might cause the collapse of the leaf lobes around their petiole, giving an aspect of a semiclosed umbrella, which has been interpreted as a protection device by some authors. In our experience the collapsing of the leaf only happens when there are several larvae together and only when they are in the 5th instar, and we consider it to be an accidental happening caused by the controlling gnawing of the ribs. The larvae, when together, do not show belligerent reactions against each other and often three to five large larvae are seen resting closely parallel to each other. The larvae of *C. dirce*, like several others belonging to other groups (among the Nymphalidae, Morphidae, Brassolidae, etc.), have a mid-ventral eversible gland placed anterad of the prothoracic legs, which is extruded when disturbed, producing a faint scent. This gland is readily noticeable during the final larval instars. Prior to pupation the larvae, if still gregarious, scatter and look for a convenient place to pupate, most of the time on the same foodplant, but also on clinging vines. At that time they stop feeding and empty their digestive tracts, ejecting a green fluid mixed with excreta.

The prepupal larvae hang from their anal prolegs, thorax incurved ventrally, for one day.

The pupae hang loosely from their pointed cremaster vertical to the ground, and swing freely at the faintest breeze or movement of the plant. This fact completes the "dry-broken-twig" effect which the shape and color of the pupae evoke, not exceeded by any other Rhopalocera. The pupae when molested react by lateral swings, always reassuming the perpendicular position. The pupae darken slightly when the adult is ready to emerge.

The adults emerge rapidly and hang from the pupa shell while expanding the wings and ejecting a rusty-brown meconium. In about 20 minutes they are ready to fly. The aggressive temperament and the striking combination of colors of this species are anything but cryptic. Larvae collected in the field while in late instars very often yield tachinid parasites.

The foodplants are Moraceae. The preferred one is a tree locally known as "Guarumo" (*Cecropia mexicana* Hmsl. and *peltata* L.), but at times another Moraceae not determined, which is shared with *Adelpha melanthe* Bates, is used. All the food-plants are rather common along ravines, road shoulders and wooded land. Both species of *Cecropia* are very similar and it would need a specialist to tell them apart. They usually have naked trunks with a few radiating branches high from the ground, each one crowned by an umbrella-like mass of long petiolated, deeply lobed (up to 13 lobes) leaves which may be over 50 cm in diameter. The trunks are hollow and often inhabited by very viciously biting ants, making an interesting case of symbiosis. According to Standley (1922) the tree is widely used in Tropical America for popular medicine due to the causticity of its fluids and its digitalis-like properties. Its sap contains also rubber but not in commercial concentration. Calderon and Standley (1941) state that the leaves of this plant mixed with salt, help deliveries of cattle. It is to be noted that the very young plants do not have peltated leaves, but entire, cordate leaves at first, which later become trilobed. When the tree has grown about 1.5 m the leaves finally grow multilobed. This fact has caused some authors to misidentify the plant, which has produced confusion about the foodplant in their reports. *Cecropia* trees are known in Brazil as "Embauba" among other vernacular names, a name that has been mentioned in several works in relation to other species of butterflies, without giving the scientific name. In El Salvador, *Cecropia* spp. are found from sea level up to about 2000 m altitude. *Colobura dirce* is also found within that range.

DISCUSSION

Colobura dirce has often been called in the literature *Gynaecia dirce* L. According to Hemming (1967) the generic name *Gynaecia* Doubleday is an objective junior synonym of *Colobura* Billberg.

Müller (1886) made a detailed description of the early stages, giving *Cecropia pachistachia* Trei as the foodplant in Brazil. According to this author, Dewitz, Stoll and Sepp had made some partial observations on the early stages also, but with many inaccuracies. The larvae and pupae are mentioned briefly by Seitz (1924) who does not however give the foodplant. Dyar (1912) also described the larva without mentioning the foodplant. All of these authors used the name *Gynaecia dirce*.

C. dirce has been classically considered to be closely related to the species of the genera *Smyrna*, *Historis* and *Coea*, as well as to others non-existent in El Salvador. *Colobura* (= *Gynaecia*) was the first one named (as *Papilio dirce* by Linnaeus, in 1758, later *C. dirce* by Billberg in 1820, and *Gynaecia dirce* by Doubleday in 1844); thence the group has been called Gynaeciidae (Seitz, 1924) or Coloburinae (Ebert, 1969). Some modern authors include some of

the species related to *Colobura* in the Subfamily Limenitinae, tribe Limenitini (Klots, 1960), or in the Subfamily Nymphalinae, tribe Limenitini (Ehrlich & Ehrlich, 1961), but they warn that the arrangement of subfamilies and tribes, as it is now, is rather a compromise, due to the incomplete knowledge about many tropical butterflies, in particular Neotropical.

We will compare the various stages of *Colobura dirce* with the equivalent stages of other Rhopalocera and specially with these of the species belonging to the alleged group of the Coloburinae.

The egg of *C. dirce*, in a very broad aspect, resembles the egg of other Nymphalidae: *Apatura* spp., *Victorina* (= *Metamorpha*) *epaphus* Latreille (Young, 1972), *V.* (= *M*) *stelenes* (Young & Muyshondt, 1973 b), and their close relatives *Anartia fatima* Fab., *A. jatrophae* Johanson, *Precis genoveva* Stoll, because they are also spherical with vertical ribs; but the eggs of these others have more ribs than those of *Colobura*: those of *Apatura* with 16 which end in a series of rounded cells around the micropyle; those of *Victorina* with 17 half of them fading before reaching the micropyle. The egg of *Historis* is spherical and has 23 ribs, which do not reach the micropylar area but form an intricate pattern of hexagons around it. The ribs of *Historis* egg in addition have a host of tiny, thin spinulets, which is an unique characteristic among the eggs of butterflies we have seen. The eggs of *Smyrna* spp. do have the same number of ribs as in *Colobura*, but the base is more flattened, which gives the eggs a different aspect. Of these species only *Colobura* deposits the eggs in clusters.

The naked, fusiform larvae of *Apatura* spp. in no way resemble the spiny, cylindrical larva of *Colobura*. The larvae of *Victorina* and related species do resemble that of *Colobura* in a superficial way, as they are cylindrical, velvety black, spiny and with long horns on the head. Under closer examination, though, we see that the horns, the shape and location of the body spines are different, and that there is an additional mesal row of spines in *Victorina*. The larvae of *Smyrna* have the head more spiny than that of *Colobura*, and are armed with short, thick horns. *S. blomfildia* also has an additional mesal row of spines (which is lacking in *S. karwinskii*). The heads of *Historis* and *Coea* resemble very much that of *Smyrna*. The body does not have the mesal row of spines, but these are shorter than in *Colobura*. The larvae of *Apatura*, *Smyrna*, *Historis* and *Coea* are solitary and have the perch-making habit. Those of *Victorina* and allies are also solitary but do not make perches. The latter feed on Acanthaceae exclusively and *Apatura* on Ulmaceae. Both *Smyrna* feed on various Urticaceae, while *Historis* and *Coea* on *Cecropia* spp.

The differences between *C. dirce* and the species mentioned are more evident in the pupae. Those of *Apatura* are green, flat and very humped dorsally. Those of *Victorina* are green, spindle-shaped with some spines protecting the

dorsal part of the abdomen. Those of *Smyrna* are brown, naked, very plump. Those of *Historis* and *Coea* (very much alike) are elongated, dorsally humped, with a row of dorsal spines along the meson, and two long head projections. As described in the life cycle, the pupa of *Colobura* is long, thin, cylindrical and light brown, in all respects like a fragment of dry twig. Among the Papilionidae we have found pupae which look also like a piece of wood, mostly in *Papilio anchisiades*, but in this case the pupa is much thicker and more or less conical and does not have appendices on the body.

The shape and coloration of the adults of the various species compared here are very different from each other, with the exception of both *Smyrna* which are much like each other in color and shape. *Historis* and *Coea* have the same coloration, but not the shape. As for behavior, the adults of *Apatura*, *Smyrna*, *Historis* and *Coea* do have many points in common with *Colobura*: fast rustling flight, tree perching, feeding habits and a pugnacious territorial defense. But it is also true that these traits are shared by many other species of genera which nobody would even think of putting together with *Colobura*, such as *Anaea* spp., *Prepona* spp., *Catonephele* spp. and many others. In this respect *Victorina* does not resemble any of the species cited at all.

A point which would seem to put *Smyrna* out of the group is its striking sexual dimorphism, not present in the rest of the species here considered. But this paradoxical difference occurs also in other well defined groups: within the Catonephelinae, we have *Catonephele numilia esite* (Muyshondt, 1973 a), *C. nyctimus* and *Epiphile adrasta adrasta* (Muyshondt, 1973 b) with strong and evident sexual dimorphism; but then we have *Temenis laothoe liberia* (Muyshondt, 1973 c), *Pseudonica flavilla canthara* (Muyshondt, 1973 d) and *Pyrrhogyra hypsenor* (Muyshondt, 1974 a) without sexual dimorphism. So the presence or absence of sexual dimorphism does not seem to be a strong criterion to determine close relationship between genera. Nor does the number of rows of spines, as otherwise two species as closely related as *S. blomfildia* and *S. karwinskii*, as evidenced in all respects except the number of rows of spines in the larval stage, would belong to different groups.

We consider it very questionable to place *Colobura*, *Smyrna*, *Historis* and *Coea* with the Limenitidi, where *Limenitis* and *Adelpha* belong without the least doubt, as they have nothing in common: shape of eggs, larvae, pupae or adults. Their behavior also show more discrepancies than resemblances. The only point in common in certain species of *Adelpha* (*melanthe* and *lerna*, in our experience), with some species of the so-called Coloburinae, is the use of Moraceae as foodplants. The rest of the *Adelpha* we have reared (*celerio*, *fessonia*, *albifilum*, *basiloides* and *iphicla*), use Rubiaceae or Melastomaceae. So this factor is not consistent either.

It is to be noted that the eversible gland located anterad of the prothoracic

legs, which is present in *Colobura dirce*, exists also in a number of other species of Rhopalocera and even in many Heterocera. In our experience we have noticed it in *Morpho peleides* and *M. polyphemus* (Young & Muyshondt, 1973 a, 1972), several species of *Anaea* (Muyshondt, 1974 b, c, 1975), *Caligo memnon*, *Opsiphanes tamarindi*, *Manataria maculata*, various species of *Taygetis* and *Chlosyne*. Müller (1886) in the chapter "Rückblick auf die Brassolinae" mentions that the larvae of Brassolinae are provided with a "Stink-wulst" (stink-pimple) which is also present in many other larvae: all Nymphalidae subfamilies, Danaidae and Hesperidae, and which apparently is lacking in Pieridae and Erycinidae. Peterson (1948) states also that such a gland is found in various larvae of Lepidoptera, and he draws several Rhopalocera larvae (*Polygonia* sp., *Euptoieta claudia* Cramer, *Nymphalis antiopa* L.) and several Heterocera larvae as well, with the gland extruded and clearly marked. According to Dr. A. B. Klots (personal communication) at least many Notodontidae larvae show that gland. We have been unable to find a name for that gland in particular, which in our observations produce a scent more or less strong, and at times very unpleasant. The dorsal V-shaped odoriferous gland of the Papilionidae larvae is called an *osmeterium*. This ventral prothoracic gland is a short, rather thick, bulbous, eversible projection of variable color, not forked. We propose the name *adenosma* for it, if it has not been previously named otherwise. (From the greek *adenos*, gland, and *osme*, smell.)

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